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Escape from the garden: spreading, effects and traits of a new risky invasive ornamental plant (*Gaillardia aristata* Pursh)

Gabriella Süle[1], Zsombor Miholcsa[2], Csaba Molnár[3], Anikó Kovács-Hostyánszki[1,4], Annamária Fenesi[2,5], Norbert Bauer[6], Viktor Szigeti[1,4]

1 *Lendület Ecosystem Services Research Group, Institute of Ecology and Botany, Centre for Ecological Research, Vácrátót, Hungary* **2** *Hungarian Department of Biology and Ecology, Babeș-Bolyai University, Cluj-Napoca, Romania* **3** *Kassai street 34. H-3728, Gömörszőlős, Hungary* **4** *National Laboratory for Health Security, Centre for Ecological Research, Budapest, Hungary* **5** *ELKH-DE Functional and Restoration Ecology Research Group, Debrecen, Hungary* **6** *Department of Botany, Hungarian Natural History Museum, Budapest, Hungary*

Corresponding author: Gabriella Süle (sulegaby@gmail.com)

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Abstract

Ornamental plants constitute a major source of invasive species. *Gaillardia aristata* (great blanketflower) is planted worldwide and its escape has been reported in several European countries without ecological impact assessment on the invasive potential. As there is a markedly spreading population with invasive behaviour in Hungary, we aimed to reveal the distribution, impacts and traits of *G. aristata*. We gathered occurrence data outside the gardens in Hungary, based on literature, unpublished observations by experts and our own records. We investigated the impacts of an extended population, where the species invaded sandy old-fields within a 25 km^2 area. Here, we compared the species richness, diversity, community composition and height of invaded and uninvaded vegetation. Furthermore, we evaluated the traits potentially associated with the invasiveness of *G. aristata* in comparison with other herbaceous invasive species in the region. We found that *G. aristata* occurred mostly by casual escapes, but naturalised and invasive populations were also detected in considerable numbers. *G. aristata* usually appeared close to gardens and ruderal habitats, but also in semi-natural and natural grasslands and tended to spread better in sandy soils. We found lower plant species richness and Shannon diversity in the invaded sites and the invasion of *G. aristata* significantly influenced the composition of the plant community. The trait analyses revealed that the invasive potential of *G. aristata* is backed by a wide germination niche breadth, extremely long flowering period, small shoot-root ratio (large absorption and gripping surface), large seeds (longer persistence) and

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dispersal by epizoochory of grazing livestock (mostly by sheep), probably helping the species' survival and spreading in the disturbed, species-poor, sandy, open habitats. These functional traits, as well as the ornamental utilisation, may act together with the aridisation of the climate and the changing land-use practices (e.g. abandoned, disturbed sites) in the success of *G. aristata*. We raise awareness of the rapid transition of *G. aristata* from ornamental plant to casual alien and then to invasive species in certain environmental conditions (i.e. sandy soils, species-poor communities, human disturbances), although it seems to be not a strong ecosystem transformer so far. Nonetheless, banning it from seed mixtures, developing eradication strategy and long-term monitoring of this species would be important to halt its spreading in time.

Keywords

alien plant species, blanketflower, casual escape, community composition, garden plant, naturalisation, occurrence map, old-field

Introduction

Unintentional and intentional human activities have the greatest role in the introduction of new species (Hulme et al. 2008; Gallien and Carboni 2017). Species introduced as a commodity (e.g. ornamental or garden plants) constitute a major source of potentially invasive species (Auer 2008). These species are artificially relocated into a new area with human help, where the required environmental conditions (e.g. watering, nutrition, pesticide control) are assured (Haeuser et al. 2019). Through these, introduced ornamental plants are able to pre-adapt to the local abiotic conditions, enhancing their chance to escape (Richardson et al. 2000; Hulme et al. 2008; Marco et al. 2010). After a potential escape, they face the barriers of the naturalisation-invasion process (Richardson and Pyšek 2012), while climatic and environmental factors, as well as functional traits of invasive species, act together to influence their success and ability to disperse (Dietz and Edwards 2006; Gallien and Carboni 2017; Haeuser et al. 2017). However, not all non-native species can survive and co-exist with the resident native species in a long term (Gallien and Carboni 2017).

Dozens of ornamental plants have been introduced from warmer climatic regions, such as the low-latitude regions of North and South America (Haeuser et al. 2019). Thus, by global warming, they will probably encounter soon the required environmental conditions on a larger scale (Bradley et al. 2010; IPCC 2021), increasing their chance of escaping and possibly becoming invasive species (Haeuser et al. 2017, 2019; Fahey et al. 2018; Cao et al. 2021). Amongst functional traits, long flowering period, large height, seed mass and total biomass, high germination rate and dispersal ability, as well as high stress tolerance, were proved to enhance the invasion potential of a plant species (Nentwig 2007; Richardson and Pyšek 2012; Gallien and Carboni 2017; Wang et al. 2018). These characteristics are also typical for the species used in horticulture because they facilitate plant establishment and growth in gardens (Marco et al. 2010). A new generation of invasive ornamental plant species is to be expected, which requires the attention of ecologists and conservationists (Bradley et al. 2010). Therefore, early warning systems are needed (Rainford et al. 2020), which monitor the escaped

ornamental plants, present regional invasion events and assess the impact of non-native species at an early stage (Hulme 2006). These actions may help to alert other countries and to detect and blacklist immediately these species (Seebens et al. 2017).

Gaillardia species were introduced as ornamental plants to Europe in the 18th century (Stoutamire 1960). The great blanketflower (*Gaillardia aristata* Pursh), a native species in North America is planted worldwide (Wiersema and León 2013). It is classified mostly as weedy or naturalised species, with a medium-level weediness rating by Randall (2017). Its spread has been reported in more than 10 European countries (Randall 2017; Roy et al. 2020) and it is reported as invasive in Russia (Vinogradova et al. 2010). In Hungary, the first escape of this species was observed in the early 20th century (Soó 1954; Priszter 1960). Balogh et al. (2004) classified it as a naturalised species, while a decade later, Korda et al. (2018) labelled it as dangerous and not recommended for planting in Hungary. In 2019, we surveyed an extended population near Izsák (Bács-Kiskun County, mid-Hungary; Molnár et al. (2003)) with invasive behaviour and considerable abundances across 25 km^2 (see Fig. 1). Due to the missing knowledge about the species' ecological impact and invasion ecology, here, we aimed to obtain information about the invasiveness of this ornamental plant species and to raise awareness.

The objectives of this study were: 1) to map the occurrence of *G. aristata* in Hungary, 2) to study the potential impacts of *G. aristata* on the vegetation and 3) to understand its invasiveness through its traits in comparison with other herbaceous non-native invasive plant species of the invaded region. For objective 1), we gathered all available information on the establishments outside the gardens from literature and experts, including our own observations. For objective 2), we compared the species richness, diversity, community composition and height of the old-field vegetation between sites invaded by *G. aristata* and their uninvaded control pairs along a coverage gradient of *G. aristata* at the above-mentioned single location. For objective 3), we compared the traits of *G. aristata* and other non-native invasive herbaceous species present in the study region to understand the role of different biological attributes in its invasive behaviour.

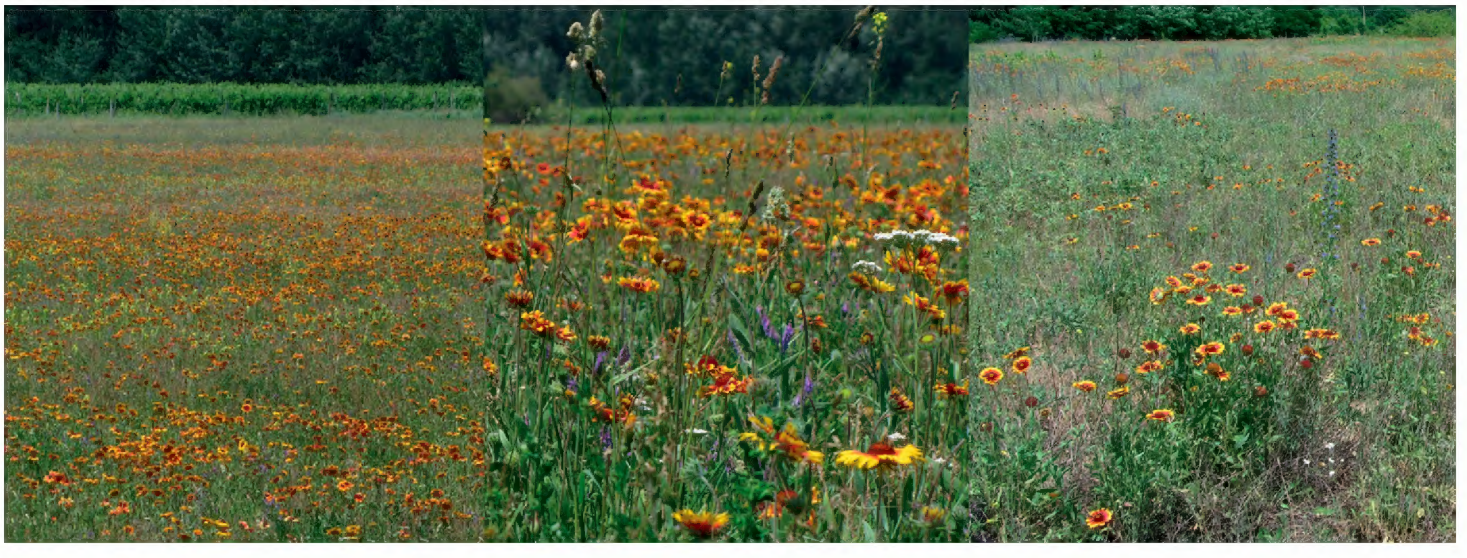

Figure 1. An extended population of *Gaillardia aristata* near Izsák, Hungary (46.791434, 19.298135) with invasive behaviour.

Materials and methods

Studied species

G. aristata is a perennial herb belonging to the Asteraceae family (Hegstad and Maron 2019), native to North America (Winslow 2011b). It is a typical species of short-grass prairie (Winslow 2011a) and prefers dry, open habitats with a Mediterranean climate (Randall 2017) due to its drought tolerance and adaptability to well-drained soils (Winslow 2011a). Its mean height is around 65 cm (Winslow 2011b). In its native range, it germinates early (April/May), blooms from the end of spring with a long flowering period and bears fruit from summer to autumn (Hegstad and Maron 2019; Kattge et al. 2020), with relatively large achenes and long hairy pappus (Winslow 2011b). The seeds' properties indicate anemochory and epizoochory (Chytrý et al. 2021), although many seeds fall directly beneath the maternal plant (Hegstad and Maron 2019). It does not reproduce with clonal spreading (Kattge et al. 2020), but can re-seed in abundance (Winslow 2011b). It is a mid-successional species establishing dense populations in disturbed areas in its native range (Taylor 1992; Winslow 2011b). A wide variety of pollinators visit *G. aristata* for pollen and nectar in its native range (Winslow 2011b) and also in Central Europe (Kovács-Hostyánszki et al. 2022).

Occurrence of *G. aristata* within Hungary

We started to map the spontaneous distribution of *G. aristata* outside the gardens in Hungary after we became aware of the invasive population in our studied area (see the next "Study site" section). We gathered the occurrence data from literature, personal communications of experts and our own records. To find current occurrences, we used the "Distribution atlas of vascular plants of Hungary" database (Bartha et al. 2022). During literature scanning, we used Arcanum Digitheca (https://www.arcanum.com/en/), MATARKA (Hungarian Periodicals Table of Contents Database, https://matarka.hu/) and ad hoc literature scanning. We contacted field experts to collect new occurrence data of this species and recorded our own observations in 2018–2022. We scanned online databases, i.e. iNaturalist (https://www.inaturalist.org/) and Pl@ntNet (https://plantnet.org/) and marked occurrences indicating high probability of escapes (i.e. the occurrence was not in a garden, while in herbaceous vegetation). We have not recorded localities where the species could be just planted out to the street front, for example, the population showed signs of care including well-kept or weeded out surroundings, regular shape etc. However, in the case of ornamental plants, it is not easy to determine whether an occurrence within a settlement is the result of human planting or spontaneous escape.

We presented the occurrence map of *G. aristata* using qGIS software (QGIS 2022). We considered the approx. 6.25 km × 5.55 km grid of Central European mapping grid system (CEU; Ehrendorfer and Hamann (1965)) for the dataset of Bartha et al. (2022)

and marked all the gathered localities of *G. aristata*. We gathered the habitat types of occurrences according to the Ecosystem Map of Hungary (http://alapterkep.termeszetem.hu/) with 20 m resolution (Agrárminisztérium 2019; Tanács et al. 2021), using qGIS. The 20-metre resolution of the Ecosystem Map of Hungary conceals some details, i.e. the exact grassland type in the urban areas. In the future, recording the exact invaded habitat type is highly recommended. Furthermore, we grouped the recently documented occurrences as: 1) casual escape, 2) naturalised and 3) invasive (based on Richardson et al. (2000)).

Invasion effects of *G. aristata*

Study site

The location of our study sites was near Izsák City, Hungary (Fig. 2B). The landscape was covered by small-scale, mostly sandy old-fields between scattered homesteads due to the declining agricultural activity (Molnár et al. 2003). A military facility has operated in this region since the 19th century (Honvédség 1897; Mesznéder 2005), which heavily influenced the natural vegetation with soil disturbances and frequent fire events (Molnár et al. 2003). According to a local pensioner, *G. aristata* was planted around the former Matyó Castle (Izsák: Matyóduló) in the 1950–60s and was transplanted from there to other gardens, from where it escaped. Molnár et al. (2003) reported the first record of its spread at the border of Izsák, without major conservation concern at that time (Sipos 2004). Today, *G. aristata* occurs in all kinds of habitats, except forests and wetlands in the neighbourhood including former croplands, but also natural and semi-natural open and closed pannonic sand steppic grasslands with the risk of further spreading (Fig. 2; Suppl. material 1). We sampled only this small locality because, in the year of sampling (2019), only our study sites near Izsák were known as invaded areas by an extended population of *G. aristata* with high abundance.

Botanical sampling

We sampled 50 m × 50 m habitat patches in seven pairs of sandy old-fields in a 5 km × 5 km landscape window in June 2019 (Fig. 2B). One of the site pairs was invaded by *G. aristata* ("invaded sites", > 10% *G. aristata* (absolute) coverage), while the other one was uninvaded ("control sites", absent or < 3% *G. aristata*). Site pairs were close to each other (median: 613 m, min–max: 189–1481 m distance between the pairs) and had similar habitat conditions.

We estimated the percent green cover of all herbaceous plant species within three 3 m × 3 m plots randomly placed within the 50 m × 50 m habitat patches. Plant species were identified by prior knowledge and by field guides (Simon 2000; Király 2009) and we used plant names according to World Flora Online (WFO 2022). We also measured the height of the local vegetation at 10 random points in all plots.

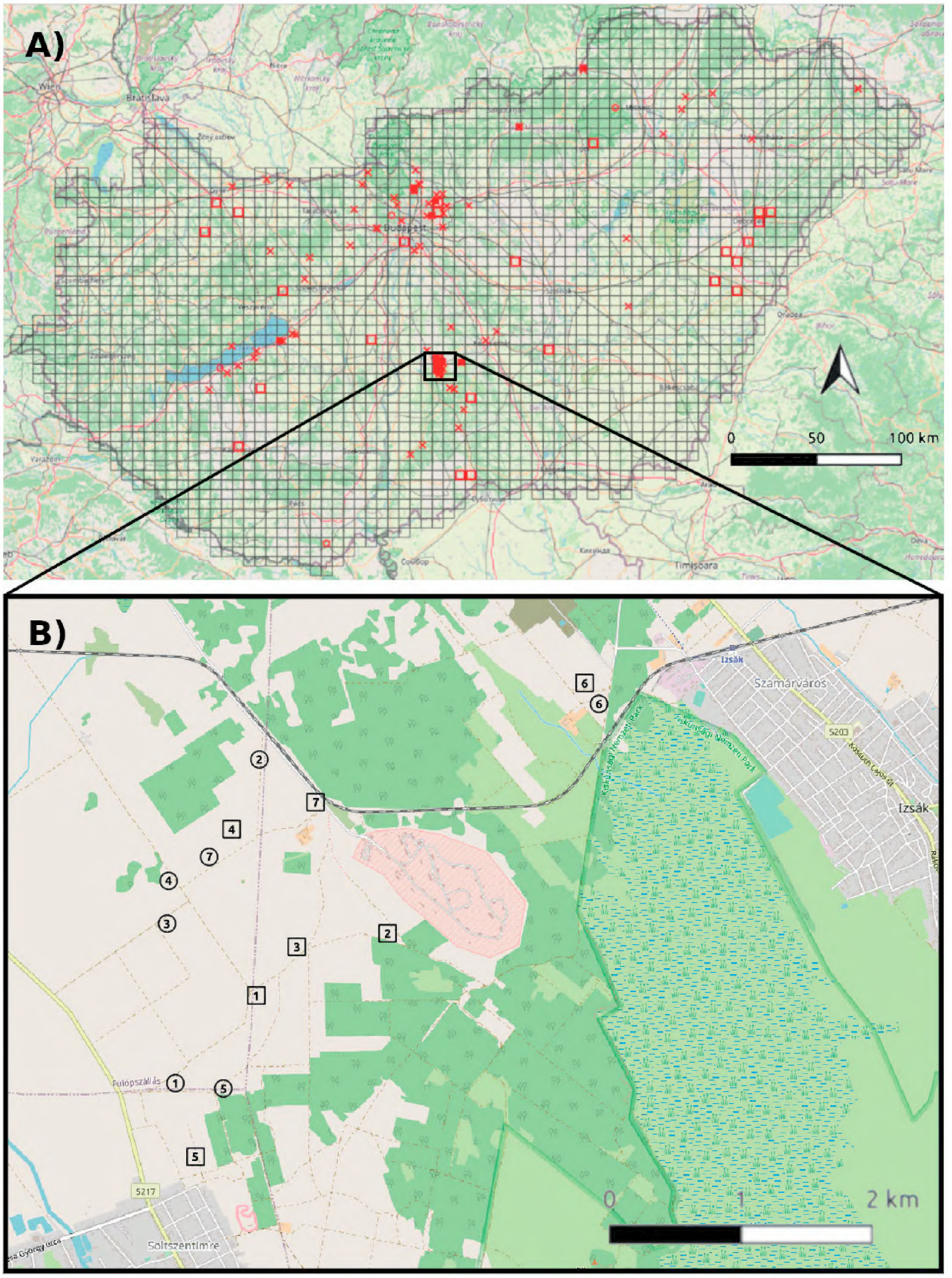

Figure 2. The occurrence of *Gaillardia aristata* within Hungary (**A**) and the sampling sites (**B**) **A** red squares represent the occurrences from the "Distribution atlas of vascular plants of Hungary" database (Bartha et al. 2022) in approx. 35 km^2 grid of "Mapping of the Central European Flora" (shown by black thin grid). Red circles represent historical data from literature. Red crosses represent casual escape, while red filled squares represent naturalised or invaded populations, based on data from online databases, own observations and personal communications by experts. We do not present three points where the species has disappeared (see details in Suppl. material 1) **B** squares represent the sampled invaded, while circles represent control sites for invasion ecology study of *G. aristata*. Numbers represent site pairs. Map data 2022 OpenStreetMap.

Statistical analyses

We analysed the data at plot-level. We obtained the species richness of plants from the cumulative number of species for each plot without *G. aristata*. We calculated Shannon diversity both including and subtracting the cover values of *G. aristata* for each plot. In this way, we differentiated between *G. aristata*'s contribution to and impact on the diversity of local plant communities (Thomsen et al. 2016). We also calculated the average of the 10 vegetation height values for each plot.

First, we analysed the differences in species richness, the two types of Shannon diversity (henceforth, the inclusion and subtraction models, respectively) and vegetation height between the invaded and control sites. The explanatory variable was the status of the sites (i.e. invaded vs. control sites). Second, we analysed the effect of *G. aristata* coverage on the species richness, Shannon diversity indices and the height of vegetation. The explanatory variable was the percentage cover of *G. aristata*. We applied generalised linear mixed models (GLMMs) with Poisson distribution for species richness and with Gaussian distribution for Shannon diversity indices and vegetation height (Venables and Ripley 2002; Zuur et al. 2009). Site pairs were built into the model as random factors. We adjusted p-values separately for response variables using the method of Benjamini and Hochberg (1995). We calculated pseudo-R^2 (Nakagawa and Schielzeth 2013) for all models.

Furthermore, we analysed the effects of invasion and the coverage of *G. aristata* on the community composition of plants with and without *G. aristata*. We applied Permutational Multivariate Analysis of Variance (PERMANOVA), using Bray-Curtis dissimilarities for species-level percentage data (Borcard et al. 2018). We included the sampled site pairs as "blocks" (i.e. random factor) to handle the non-independencies in the sampling structure. We adjusted p-values separately for response variables using the method of Benjamini and Hochberg (1995). We also performed non-metric multidimensional scaling (NMDS; Borcard et al. (2018)) to reveal the pattern of the coverage of *G. aristata* in the plant communities. We presented the first two dimensions of NMDS. We generated smooth surfaces along the coverage gradient of *G. aristata* with generalised additive models (GAMs) to interpolate the fitted values on the NMDS plot. We also evaluated the association of plant species (without *G. aristata*) to invaded or uninvaded sites by indicator species analysis (Borcard et al. 2018). The indicator values of the species were tested via the Monte-Carlo simulation using 10,000 permutations. The accepted significance level was $p < 0.05$.

The statistical analyses were carried out using the R v.3.6.3 statistical environment (RCoreTeam 2020), "glmmTMB" v.1.1.2.3 and "performance" v.0.8.0 packages for GLMMs (Brooks et al. 2017; Lüdecke et al. 2021), "vegan" v.2.5-6. for PERMANOVA (Oksanen et al. 2019) and "labdsv" v.2.0-1 packages for indicator species analysis (Dufrêne and Legendre 1997).

Traits of *G. aristata* and non-native herbaceous invasive species

In order to understand the invasion mechanism of *G. aristata*, its biological traits were measured. To interpret the invasiveness of this species, by descriptive statistics, its traits

were compared to other herbaceous non-native invasive species from our studied region (based on Balogh et al. (2004)): *Ambrosia artemisiifolia* L.; *Asclepias syriaca* L.; *Erigeron annuus* (L.) Pers.; *E. canadensis* L.; *Helianthus tuberosus* L.; *Impatiens glandulifera* Royle; *Oenothera villosa* Thunb.; *Phytolacca americana* L.; *Reynoutria japonica* Houtt.; *Solidago canadensis* L.; *S. gigantea* Aiton; *Xanthium strumarium* subsp. *strumarium*. The chosen non-native invasive species are highly successful in the studied region, but their success is backed by different trait syndromes and ecological strategies. We might identify crucial traits with outstanding trait values that define the possible invasive strategy of *G. aristata* by comparing them along the traits usually associated with invasiveness (van Kleunen et al. 2010). For this (and other purposes), we collected traits of East European invasive plants for a comprehensive trait database (Fenesi et al., unpublished data). This is the nearest, available database which contains a series of functional traits of all important herbaceous invasive plants of the region.

To test the optimal timing of germination for each species, we collected seeds and fruits ("seeds" for the sake of simplicity) of these species from invasive populations in Transylvania, Romania in the summer and autumn of 2020, from at least 30 individuals of one population, mixed and kept in paper bags. We calculated the germination rate (%) for all invasive species in three germination conditions (autumn, early spring and late spring). In the temperate climate of Europe, plant species' seeds germinate in autumn (species with seeds without dormancy, for example, many annuals, biennials or species of disturbed habitats) or in spring (species that need a short or long chilling period to break the seeds' dormancy; Walck et al. (2011)). Therefore, we simulated these conditions to offer the species the possibility to show how wide their germination niches are. Seeds were put to germinate in autumn, after dry-storage for one-two months and in spring, after cold-wet stratification in the dark at temperature of 1–4 °C for three months. Five replicates of 20 seeds were placed in plastic Petri dishes filled with two filter papers for each treatment. The sealed dishes with fresh seeds were put in germination chambers (Sanyo MLR-352H; Sanyo/Panasonic Healthcare Co., Ltd, Japan.) in October 2020, simulating autumn conditions (11 hours light at 15 °C, 13 hours darkness at 5 °C); while stratified seeds were placed in germination chambers in April 2021, simulating early spring conditions (13 hours light at 15 °C and 11 hours darkness at 5 °C) or late spring conditions (14 hours light at 20 °C and 10 hours darkness at 10 °C). The Petri dishes were regularly watered with distilled water and monitored three times a week; all germinated seeds were recorded and removed.

To present the average height (cm) and the beginning and duration of flowering (month) of invasive species, we gathered the data on the minimum and maximum height and the flowering phenology from a Hungarian field guide (Király 2009). For *G. aristata*, we used Flora of North America (Strother 2020). Most of the biennials and perennials did not flower in the pots during our one vegetation season experiment, so we could not use these data.

To calculate the shoot-root ratio, total biomass (g) and specific leaf area (mm^2/mg), seeds were put to germinate in 1-litre pots, filled with potting soil. The emerging seedlings (one per pot, ten replicates for each species) were allowed to grow exactly eight weeks after the first true leaves were observed. The pots were watered twice a week with the same

amount of water, depending on the weather conditions: more in sunny and warm weeks and less on rainy and cloudy days. We intended to set up an optimal water condition, i.e. not just to wet the soil on the surface, but to give enough water to the whole pot. This meant about 80% of field capacity. The experiment took place in an open-air facility with transparent roof in the University Botanical Garden in Cluj-Napoca, Romania. After two months of growth, shoots with leaves and roots were separated for five plants per species, washed and dried in an oven for 48 h at 65 °C and were weighed to calculate shoot-root ratios and total biomass. Three-five plants were allowed to grow till maturity and served to calculate specific leaf area (SLA, leaf area per unit leaf mass, mm^2/mg) for each species. We collected three-five mature, but non-senescent leaves from each individual. Leaf area was calculated based on photographs of leaves using ImageJ software (Abràmoff et al. 2004). Leaves were dried for 48 h at 65 °C and weighed.

Seed mass (g) was obtained by weighing three sets of 100 seeds from each species, using an analytical scale (Kern ABJ 80- 4NM, with 0.1 mg resolution). We calculated the average weight of one hundred seeds.

The terminal velocity (m/s) of the seeds, i.e. the maximum rate of fall, expressed the wind-dispersal ability. We measured the duration of seed descent and we divided the height of fall (1.47 m) by the duration of fall by the methods of Andersen (1992). The lowest value of terminal velocity expresses the highest ability of seeds to be dispersed by wind (Ruprecht et al., unpublished data).

Epizoochory (%) was tested as the likelihood of seeds attaching to sheep fur. We focused on sheep due to their likely presence in the studied landscape and to be a possible vector of propagules. We followed the protocol of Moravcová et al. (2010): a wooden frame was covered with sheep fur and the fur was pressed to a plain surface with seeds spread over it. After three circular movements of the frame pressed to the surface, the number of propagules attached to the fur was counted. For each species, four replicates of 25 propagules, thus 100 propagules altogether were involved. Please note: terminal velocity and epizoochory are available only for 10 from the 13 investigated species.

Results

Occurrence of *G. aristata* within Hungary

For *G. aristata*, we gathered 119 occurrences altogether in 89 (3%) approx. 35 km^2 CEU cells all over Hungary. We found 27 records (26 CEU cells) in the database of Bartha et al. (2022), four historical records in four CEU cells (Soó 1954; Priszter 1960) and five occurrences (five CEU cells) from online databases (Fig. 2A; Suppl. material 1). We could supplement these data with 83 recently documented records (54 CEU cells) by personal communications of experts and own observations (Fig. 2A; Suppl. material 1). The habitat types of *G. aristata* occurrences were urban area in 28.6% (incl. green urban area with/without trees, low building, other paved or non-paved artificial area, paved road, railway), semi-natural herbaceous vegetation in 27.7% (incl. closed/open sand steppe, closed grassland in hills and mountains, salt steppe and

meadow, other herbaceous vegetation), cropland in 10.9% (incl. arable land, vineyard, complex cultivation pattern with/without scattered buildings), woodland in 4.2% (incl. black locust-dominated mixed plantation, other ligneous vegetation, woodland) and unknown in 28.6% of the total number of occurrences. The occurrences were casual escapes in 55.5%, naturalised in 6.7%, invasive population in 16.8% and unknown in 21.0% of the total number of occurrences. The "unknowns" refer to disappeared populations and the lack of exact coordinates in literature or the online database.

Invasion effects of *G. aristata*

We recorded 110 plant species in total in our study sites, 23–45 (min–max) species per site (without *G. aristata*). The average height of the local vegetation was 39.8 cm in both the invaded and control sites. The plots of invaded sites were covered 11–70% (mean: 34.8%) by *G. aristata*. We found slightly lower plant species richness in invaded sites compared to the controls (adjusted p-value = 0.080; Fig. 3; Suppl. material 2). We did not find any effect of invasive coverage on the plant species richness (adjusted p-value = 0.095; Suppl. material 2). Shannon diversity was significantly lower in the invaded sites (adjusted p-value = 0.008) and decreased with increasing *G. aristata* cover in the inclusion models (adjusted p-value < 0.001). On the contrary, there was no significant difference (adjusted p-value = 0.530) between the invaded and control sites and the cover of *G. aristata* had no significant effect on Shannon diversity in the subtraction models (adjusted p-value = 0.530). There was no significant difference between the control and invaded sites in the height of local vegetation (adjusted p-value = 0.996) and the cover of *G. aristata* had no significant effect on the vegetation height (adjusted p-value = 0.996; Fig. 3; Suppl. material 2).

We found significant differences in community composition between invaded and control sites in the inclusion models (adjusted p-value < 0.0001; $R^2 = 0.25$) and also in the subtraction models (adjusted p-value = 0.0004; $R^2 = 0.07$; by PERMANOVA; Fig. 4). Furthermore, we found that the cover of *G. aristata* had a significant effect on the community composition in the inclusion (adjusted p-value < 0.0001; $R^2 = 0.23$) and in the subtraction models (adjusted p-value = 0.0006; $R^2 = 0.07$; by PERMANOVA; Fig. 4). The analysis of indicator species regarding invasion showed that four species were linked to invaded and eleven species to control sites (Table 1).

Traits of *G. aristata* and non-native invasive herbaceous species

Compared to the other more common non-native invasive herbaceous species in the region, *G. aristata* had an outstandingly high germination ratio both in autumn and during spring, showing a wide germination niche breadth (Fig. 5). Its flowering period was also extremely long and started very early compared to other species (Fig. 5). Regarding its stature, it is the shortest plant amongst the studied invasive species, thus its biomass was also small, but it invested considerably more energy in roots compared to aboveground parts. Seeds were proved likely to be dispersed by animals and less likely by wind (Fig. 5).

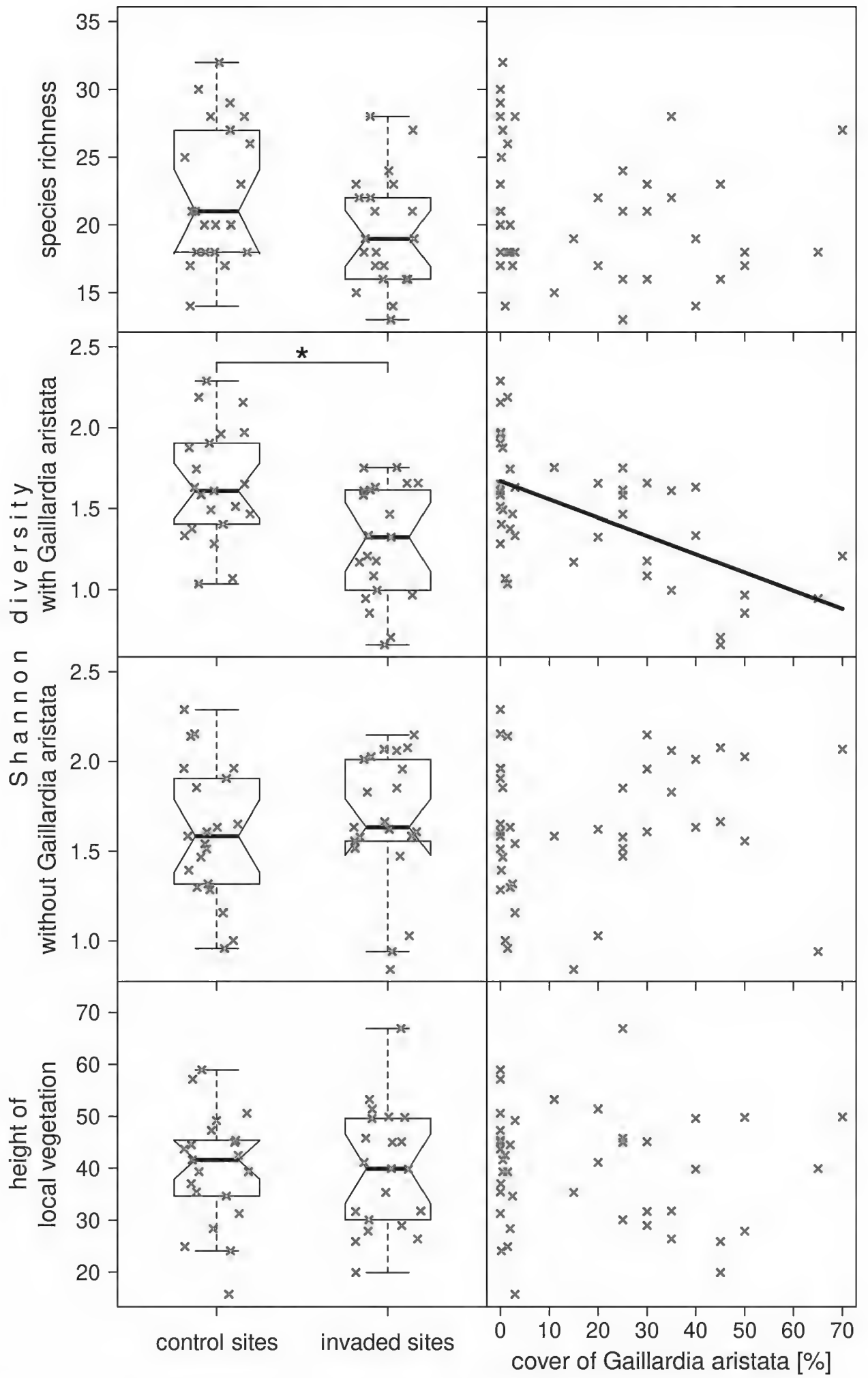

Figure 3. Effects of invasion (control vs. invaded) and cover of *Gaillardia aristata* on species richness, Shannon diversity (with and without *G. aristata*) and the height of local vegetation. Box plots show medians, lower and upper quartiles, notches show 95% confidence intervals. Grey × symbols represent sampling plots. Significant differences (after p-value adjustment) between the invaded and control sites are indicated by star (*) above the boxes and the significant effect of invasion cover by continuous lines according to the GLMMs (see Suppl. material 2).

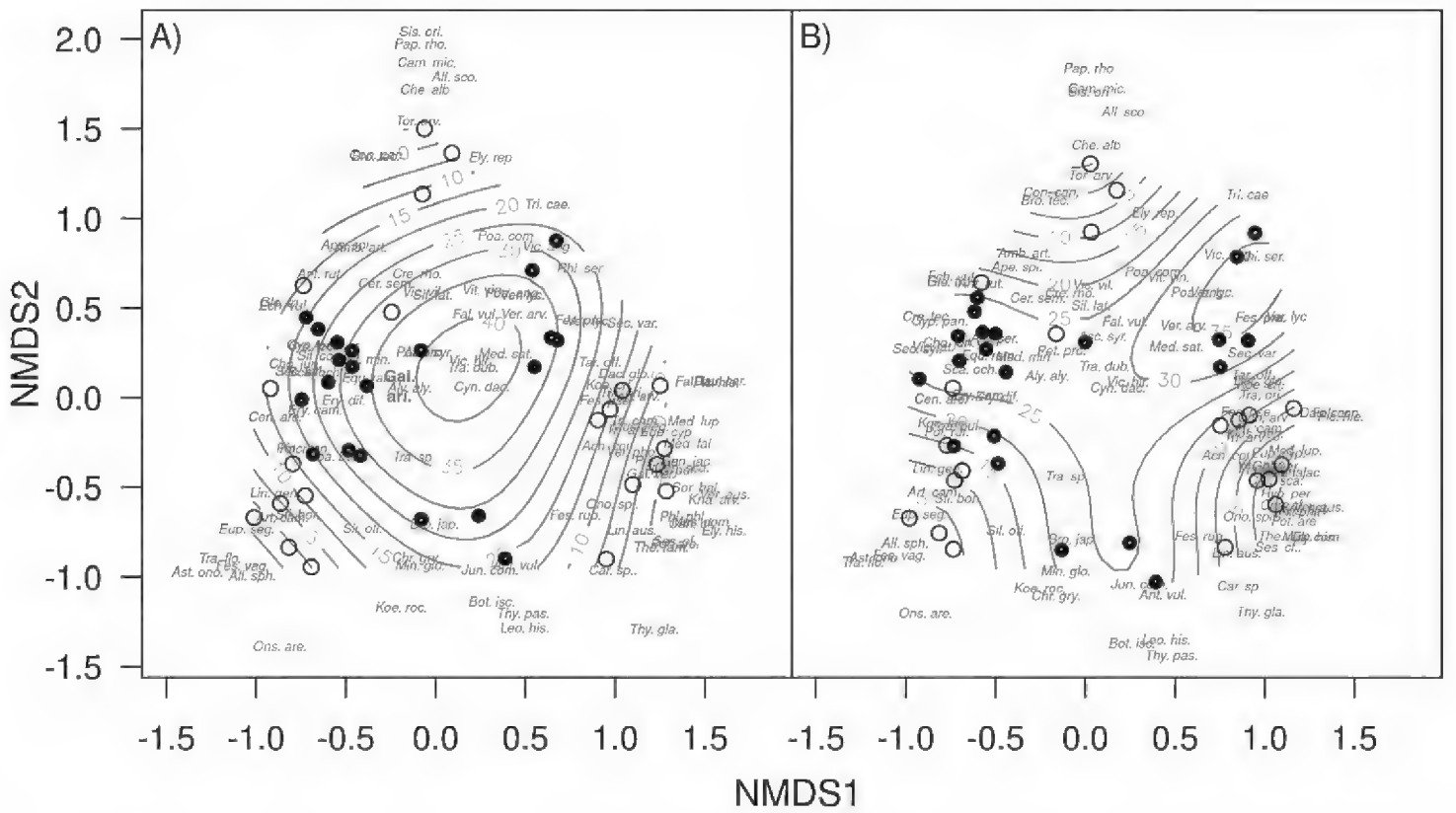

Figure 4. Community composition by NMDS ordination **A** including *Gaillardia aristata* and **B** excluding *G. aristata*. Filled circles represent the plots of invaded sites, while empty circles are the control sites. GAM fitted isoclines represent cover percentages of *G. aristata*. The italic abbreviated names indicate the plant species. *G. aristata* is highlighted by bold and larger font size on **A** part of the Figure.

Table 1. The results of analysing indicator species regarding *Gaillardia aristata* invasion. The accepted significance level was $p < 0.05$.

Species	*p*-value	IndVal	Control	Invaded
Control sites				
Centaurea scabiosa L.	0.001	0.473	0.476	0.048
Crepis foetida subsp. rhoeadifolia (M.Bieb.) Čelak.	0.036	0.556	0.571	0.381
Cynodon dactylon (L.) Pers.	0.002	0.749	0.810	0.571
Erigeron canadensis L.	0.026	0.332	0.333	0.143
Euphorbia cyparissias L.	0.004	0.381	0.381	0.000
Euphorbia seguieriana Neck.	0.046	0.271	0.286	0.095
Festuca rupicola Heuff.	0.016	0.398	0.429	0.143
Festuca vaginata Waldst. & Kit. ex Willd.	0.019	0.285	0.286	0.048
Galium verum L.	0.018	0.368	0.381	0.095
Plantago lanceolata L.	0.034	0.413	0.429	0.190
Securigera varia (L.) Lassen	0.009	0.333	0.333	0.000
Invaded sites				
Chondrilla juncea L.	0.008	0.457	0.143	0.571
Medicago sativa L.	0.043	0.271	0.048	0.286
Secale sylvestre Host.	0.021	0.457	0.238	0.476
Vicia villosa Roth	0.038	0.475	0.238	0.571

Discussion

Ornamental plants pose a great risk of escaping and turning into invasive species under human disturbances and climate change (Auer 2008; Hulme et al. 2008; Bradley et al. 2010; Klonner et al. 2019). *G. aristata* is a widely planted ornamental species, its

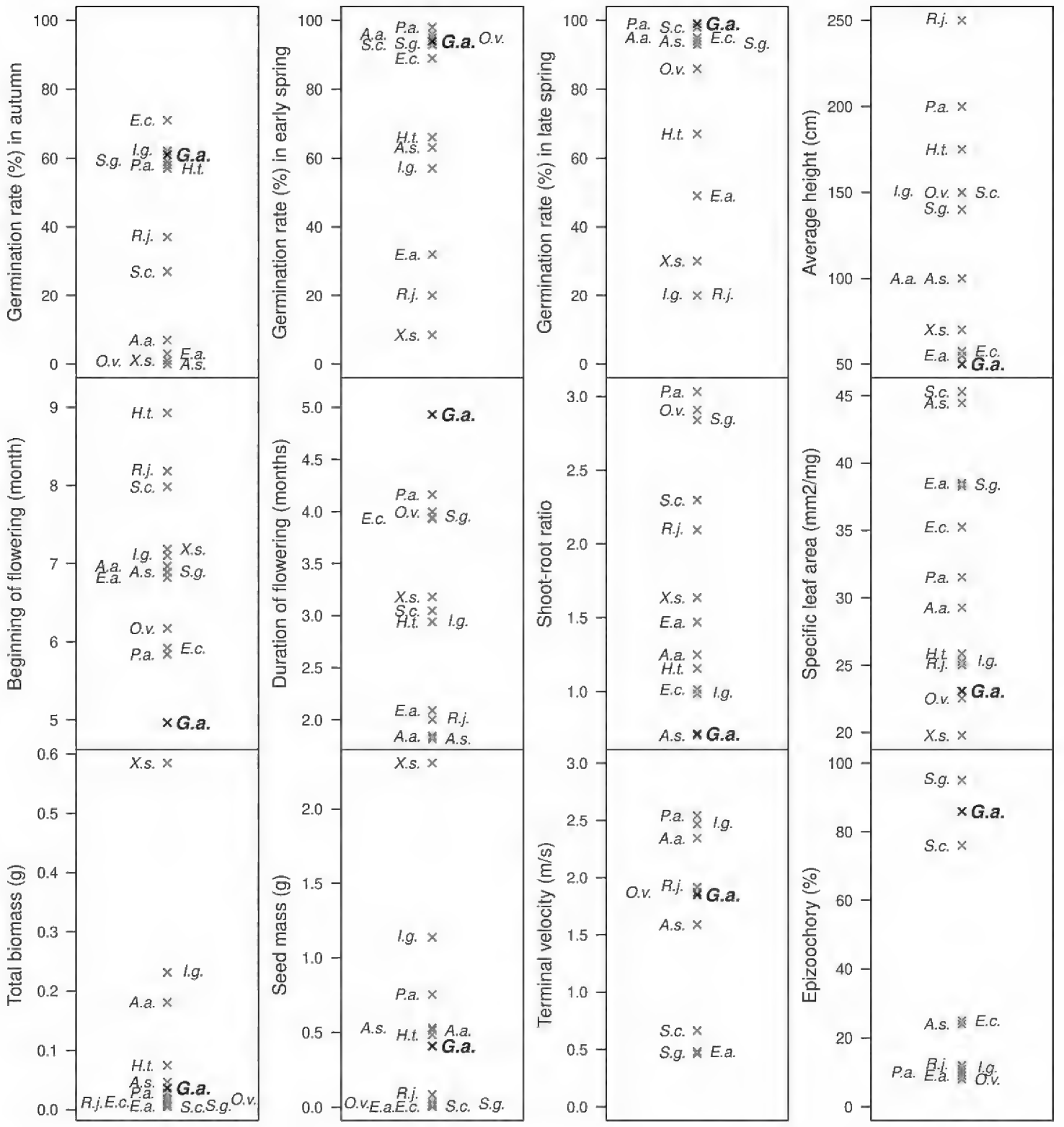

Figure 5. Traits distribution of the non-native invasive herbaceous species. The trait comparison between *Gaillardia aristata* (*G. a.*) and other invasive herbaceous species in the region: *Ambrosia artemisiifolia* (*A. a.*); *Asclepias syriaca* (*A. s.*); *Erigeron annuus* (*E. a.*); *E. canadensis* (*E. c.*); *Helianthus tuberosus* (*H. t.*); *Impatiens glandulifera* (*I. g.*); *Oenothera villosa* (*O. v.*); *Phytolacca americana* (*P. a.*); *Reynoutria japonica* (*R. j.*); *Solidago canadensis* (*S. c.*); *S. gigantea* (*S. g.*); *Xanthium strumarium subsp. strumarium* (*X. s.*). The x-axes only present the abbreviations of the investigated species, while the × symbols represent the exact trait values along the y-axes.

escape and naturalisation having been repeatedly reported before (Molnár et al. 2003; Randall 2017; Korda et al. 2018; Roy et al. 2020), but its invasive behaviour is relatively unknown (except in Russia; Vinogradova et al. (2010)). Meanwhile, in the past few years, this species presented a rapid transition from naturalisation to invasion in Hungary. Therefore, our aim was to document the circumstances of this invasion phenomenon by assessing the ecological impact of *G. aristata*, in order to raise awareness of a potential future spread in Eurasia as well.

Occurrence of *G. aristata* within Hungary

G. aristata was found in 89 (3%) approx. 35 km^2 CEU cells all over Hungary, based on the former (26 cells by Bartha et al. (2022) and four cells by historical data from literature) and recently documented (59 cells; including online databases) occurrence data. *G. aristata* occurred mostly in sandy and other loose textured soils, usually close to gardens and in other man-made or ruderal habitats. However, it was also observed in natural and semi-natural sandy grasslands and even in humid loess grasslands. There were localities where it escaped and spread, but then declined or disappeared from one year to the next due to building construction (e.g. in Erdőkertes; own observation) or without any known reason (e.g. in Soroksár Botanical Garden; Mária Hőhn ex lit.). In many locations, it was present sporadically for years, but was not able to spread aggressively (own observations). In many places (e.g. on roadsides), it was probably maintained by human disturbances (Taylor 1992; Winslow 2011b). Invasive populations were about 17% of the occurrences that might be potential hotspots of further spread to nearby native habitats. As well, there is the threat that any naturalised population or even some casual escapes may be able to transform into invasive.

Other *Gaillardia* species (Indian blanketflower (*G. pulchella* Foug.) and their hybrid (*G.* × *grandiflora* Van Houtte)) also escape from gardens and spread in Europe (Randall 2017). Together with *G. aristata*, they are challenging to identify due to similar phenotypic characteristics and their highly variable flowers (Hammond et al. 2007; Lengyel 2022). However, the three taxa differ slightly in their life cycles (Stoutamire 1960) and, while the other two taxa show only casual escapes in Hungary (personal observation; Bartha et al. (2022)), *G. aristata* escapes more often, establishing naturalised and invasive populations and seems to spread vigorously.

The impact of *G. aristata* on invaded plant communities

In our studied population, *G. aristata*'s invasion had only a moderate negative impact on the sampled old-field vegetation, suggesting only a slight potential inhibition on the distribution and growth rate of local species, as well as some potential changes in succession (Levine et al. 2003; Csecserits et al. 2011; Powell et al. 2011; Pyšek et al. 2012). Based on our results, this species is not a strong ecosystem transformer in old-fields. However, invasive species are able to slow down or halt secondary succession hindering the recovery towards semi-natural grassland vegetation (Cramer et al. 2008; Fenesi et al. 2015). The cover of an invasive species can often explain its effects on the local vegetation (Hejda et al. 2009). Moderate cover in general (such as in the case of *G. aristata*) usually results in a minor effect on the plant community compared to non-native plants with high coverage (Csecserits et al. 2011; Albert et al. 2014). However, even moderate invasion could affect other related communities, for example, pollinators. Comparing the same invaded and non-invaded old-fields, *G. aristata* had a significant effect on the abundance and diversity of hoverflies, on the abundance of honeybee and on the community composition of floral resources (Kovács-Hostyánszki et al. 2022).

The community composition and indicator species analyses of invaded and non-invaded sites suggested three different types of non-invaded old-field. Such differences can be originated from the initial seed bank, land-use history, time since abandonment as arable land, current management and the process of succession (Inouye et al. 1987; Csecserits et al. 2011). The indicator species for control sites, such as *Festuca rupicola* Heuff., *F. vaginata* Waldst. & Kit. ex Willd. and *Secale sylvestre* Host., are the dominant grass species of the closed, the perennial open and the annual open sandy grasslands (Borhidi et al. 2012), respectively, indicating two target grassland communities and a disturbed annual association during old-field succession. The invaded sites were in an intermediate phase in species composition between the mentioned grassland types (Borhidi et al. 2012). Based on these species characteristics, our study was carried out on different types of species-poor old-fields, indicating also the influence of successional pathways on the community composition. This difference amongst study sites may be an outcome of the higher beta diversity within control sites compared to more homogenised invaded sites (Socolar et al. 2016), reducing the opportunity to detect differences in diversity and in community composition.

It has to be acknowledged that this was an observational and not an experimental study; hence, we were only able to take a snapshot of the invasive behaviour of *G. aristata*. Furthermore, our study covered a relatively small area at a given location compared to the country- (and even continent-)wide distribution and the potential long-term changes of this species. We cannot rule out the possibility that the chosen control and invaded sites differed in some aspects before the invasion (e.g. differences in land-use), facilitating the spread of *G. aristata* (Davis et al. 2005). However, we did our best to choose sites with similar site conditions as possible and we assumed that the control and invaded sites differed only in the presence of *G. aristata*. The presence of this species is relatively new to the region, as well as *G. aristata* spreading as a frontline in the studied region (pers. comm. of Csaba Bíró, the Ranger of the National Park near Izsák). Here, *G. aristata* occurs in all kinds of habitats, except forests and wetlands in the neighbourhood. Based on our field experiences, we hypothesise that the possible differences between the sites may not exclude the possibility of invasion, just influence the abundance of this species in the invaded areas and the timing of invasion for the not yet invaded dry ecosystems. Nevertheless, the impact of *G. aristata* was found not really hazardous compared to the general effects of the real transformer invasive plant species (Vilà et al. 2011; Qi et al. 2014). However, an extended study would be needed to investigate the long-term effect of *G. aristata*, which might become stronger (e.g. *A. syriaca*; Csecserits et al. (2016)), stagnant or weaker (e.g. *A. artemisiifolia*; Csecserits et al. (2009)) during succession.

Traits and environmental conditions drive the invasion

According to our knowledge, our study area is the first location where the invasive behaviour of *G. aristata* has been studied. Therefore, the drivers behind the invasive mechanism are important to understand. We aimed to find out how this potentially

invasive species might be similar to other, more successful invasive species in this region and which traits of *G. aristata* might explain its invasion and success in certain habitats. *G. aristata* germinates early with resistance to allelopathic chemicals (Tyrer et al. 2007). Meanwhile, it can re-seed even in the same season (own field observation) due to its wide germination niche breadth and the mild autumn weather by the warming climate (Haeuser et al. 2017). Its chance of survival is further increased by its drought tolerance and adaptability to well-drained soils (Winslow 2011b). *G. aristata* has low SLA, which can help to maintain plant water status during drought, increasing its drought tolerance (Nautiyal et al. 2002; Girdthai et al. 2010). The small shoot-root ratio of this species indicates significant allocation to roots compared to aboveground parts of the plant, which provides large absorption and gripping surface (Noordwijk and Willigen 1987), facilitating the colonisation and spreading in loose-textured soils, such as sand. The species has no known allelopathic effect (Kattge et al. 2020), but *G. aristata* probably grows faster and taller (see Fig. 5) than most of the local species in sandy vegetation (see the average vegetation height in control sites). Thus, *G. aristata* may inhibit or delay the growth of seedlings of other species by shading and reducing water availability (Levine et al. 2003). In contrast, the larger seeds of this species (Hegstad and Maron 2019), which is non-typical for invasive plants (Rejmánek and Richardson 1996; Radny et al. 2018), could be disadvantageous in spreading. However, it can disperse well with epizoochory (Baltzinger et al. 2019), probably by sheep as well as by the main cattle species in the study area (Molnár et al. 2003). Thus, it has a continuous local seed rain with a slow, but steady seed spread-rate (Kattge et al. 2020) along with the possibility that large seeds are able to sustain the seedling under poor conditions with sufficient nutrient tissue (Jakobsson and Eriksson 2000).

G. aristata was in lag phase for several decades (Pyšek and Hulme 2005), but now it certainly encountered its required environmental conditions in this area (Haeuser et al. 2017, 2019) by climate change (i.e. warmer, arid climate (Winslow 2011b)) and human disturbances (Bradley et al. 2010; IPCC 2021) facilitating its spreading (Haeuser et al. 2019; Klonner et al. 2019). Land-use changes (i.e. land abandonment) produce suitable species-poor and disturbed habitats for this mid-successional species (Davis 2009; Winslow 2011b). Additionally, *G. aristata*'s cover was increased after wildfire events in its natural habitat (Antos et al. 1983), the short-grass prairie (Winslow 2011a) that is heavily controlled by fire (Wright and Bailey 1981). In our study region, the frequent fire events by military activities (i.e. firing range and training ground) and the potential grazing of abandoned old-fields by sheep (Molnár et al. 2003) may explain why *G. aristata* has been able to spread and shows invasive behaviour in this area. Besides these habitat conditions, also people and pollinators may admire and help to sustain this ornamental plant, due to its beauty, long flowering period and resources as a bee pasture (Lindemann-Matthies 2016; Kovács-Hostyánszki et al. 2022).

In summary, the climatic and environmental factors (aridisation of the climate and dry, nutrient-poor, rapidly warming sandy surfaces), the land-use (abandoned, probably burned arable fields), the competitive functional traits (drought tolerance, long flowering period, large roots and seeds) and the ornamental utilisation of *G. aristata* seem to act together to influence its success and ability to disperse and to become a

new, dangerous invader in dry, species-poor habitats (Molnár et al. 2003; Dietz and Edwards 2006; Gallien and Carboni 2017; Haeuser et al. 2017; Korda et al. 2018). However, uncovering the details behind a species changing into an invasive is worth further investigations. For example, revealing the differences between invasive and casual populations in traits (e.g. chemical composition; Cappuccino and Arnason (2006)) and environmental parameters (e.g. soil type) and investigating the further effect of climate change on the spreading (Mojzes et al. 2020; Orbán et al. 2021).

Conservational recommendations

For all newly-established non-native species, monitoring, ecological impact assessments and also experiments on eradication should be required (Gallien and Carboni 2017). For *G. aristata*, it would be important to carry out eradication experiments to investigate the detailed invasion biology and the opportunity to inhibit the further spreading (Hulme et al. 2008; Bradley et al. 2010). As *G. aristata* does not reproduce clonally (Kattge et al. 2020), ploughing the invaded area and then over-seeding it with a seed mixture of native species probably can be an appropriate eradication strategy in old-fields (Holt 2009). However, the longevity and persistence of *G. aristata* seeds in the seed bank are unknown. If the seed bank of *G. aristata* is persistent, it will probably remain for years (as for example, *A. artemisiifolia* Milakovic and Karrer (2016)). Hence, both the seed longevity and the seed bank persistence in the field, as well as the effect of the different eradication methods need further studies. Grazing is a questionable potential solution (Holt 2009; Winslow 2011b). Light grazing did not affect *G. aristata* (Daubenmire 1970), while it decreased by vigorous sheep and increased by cattle grazing in its original place of residence (Mueggler and Stewart 1980). However, heavy grazing is not a suitable conservation treatment for dry grasslands (Deng et al. 2014; Molnár et al. 2020); moreover, the grazing animals could play a role in its spreading in the neighbourhood. Hence, exploring the effectiveness and indirect influences of different grazing and mowing regimes is necessary.

The example of *G. aristata* spectacularly identifies that one of the most common sources of plant invasion is ornamental planting (Auer 2008; Pyšek et al. 2017). The European Union maintains a blacklist of invasive species (European Parliament 2014); however, it includes only a few species, which may require regular revision and misses species that are only later found to be problematic (Seebens et al. 2017). A list of discouraged ornamental plants, including frequent escapers and aggressive spreaders, would be needed to raise the attention of gardeners at least. The sale of *G. aristata* alone or in ornamental seed mixtures should be banned in Eurasia, especially in regions with sandy habitats.

Conclusion

In this study, we investigated the occurrences, ecological impact and traits of a new, risky, invasive, ornamental plant species, *G. aristata*. This species escaped and spread in disturbed, semi-natural and natural habitats. Although the invasion of *G.* × *grandiflora*

has already been observed in Belgium (Branquart et al. 2007; Verloove et al. 2020), it seems that in Central Europe *G. aristata* also crosses the threshold of invasion and may start to spread in the East European steppe and further. Our work demonstrated only a moderate negative impact on the old-field vegetation; so far, *G. aristata* is not a strong ecosystem transformer. Besides reviewing its phenological and morphological traits supporting the invasive behaviour, some questions remained unanswered; thus further thorough studies are needed to evaluate the exact causes behind its transformation into invasive. More attention should be paid to *G. aristata*, because there is a chance of spreading and becoming invasive elsewhere in certain (i.e. sandy, species-poor, disturbed) conditions. This ornamental species is planted and nursed in many locations (e.g. gardens, parks and facilities); hence, it can escape from many more places in the future, while people also contribute to the invasion process (Lindemann-Matthies 2016). Thus developing effective eradication strategy and long-term, continuous, systematic mapping within Eurasia would be important to reveal and halt the spreading of *G. aristata* (Hulme 2006; Royimani et al. 2019; Papp et al. 2021).

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Supplementary material 1

Occurrence of *Gaillardia aristata* within Hungary

Authors: Gabriella Süle, Zsombor Miholcsa, Csaba Molnár, Anikó Kovács-Hostyánszki, Annamária Fenesi, Norbert Bauer, Viktor Szigeti

Data type: table (Xlsx file)

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Supplementary material 2

The results of mixed models analysing the effects of the invasion and the coverage of *Gaillardia aristata* on the species richness, Shannon diversity and the height of local vegetation

Authors: Gabriella Süle, Zsombor Miholcsa, Csaba Molnár, Anikó Kovács-Hostyánszki, Annamária Fenesi, Norbert Bauer, Viktor Szigeti

Data type: table (Docx file)

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